

## Changes in Phytoplankton Size-class Abundance and Species Composition Coinciding with Changes in Water Chemistry and Zooplankton Community Structure of Lake Michigan, 1983 to 1992

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**ABSTRACT.** Phytoplankton and zooplankton were collected at offshore sites of Lake Michigan during 37 cruises in the spring and summer from 1983 to 1992. For the period, 39 common phytoplankton species accounted for 96.0% of the total abundance and 85.6% of the biomass. Over the 10-year study, the lake-wide average spring and summer phytoplankton biomass in the pelagic waters ranged from 0.27 to 1.2 g/m<sup>3</sup> (mean  $\pm$  S.E. = 0.54  $\pm$  0.03 g/m<sup>3</sup>) and phytoplankton abundance ranged from 5,132 to 39,780 cells/mL (mean  $\pm$  S.E. = 18,291  $\pm$  822 cells/mL). Mesotrophic diatoms accounted for 47.2% of the total phytoplankton biomass. The lack of a trend in the ratio of mesotrophic to eutrophic diatom indicator species suggested that no change in trophic status of the pelagic region occurred during the 1983 to 92 period; that is, the water quality of the offshore of Lake Michigan did not change. A year-to-year shift in dominance from one mesotrophic diatom species to another was evident.

Over the 10-year period, flagellates accounted for 52.2% of the summer phytoplankton biomass. The data support the concept of a shift in summer species composition away from blue-green algae dominance to flagellates prior to 1982. However after 1987, the relative importance of the > 70  $\mu$ m size class increased to over 21% of the phytoplankton abundance in the spring and over 55% in the summer. In particular, the colonial blue-greens, *Anacystis* and *Aphanothece*, became substantially more prevalent during the summer, while the flagellates, *Chromulina* and *Ochromonas*, decreased in abundance.

The changes in the relative abundance of phytoplankton size classes and species composition were examined to determine if they correlated with either the top-down mediated changes in the zooplankton community during the 1980s and 1990s or with any bottom-up variability in nutrient chemistry. Canonical correspondence analysis (CCA) suggested a significant portion of the variability of the spring and summer phytoplankton size classes from 1983-1992 (88.0% and 99.2%, respectively) was explained by environmental axis 1. Primary determinants of relative abundance of phytoplankton size class included nutrients (silica, total phosphorus, and N:P ratio) and abundance of some species of zooplankton. Specifically, *Diaptomus minutus*, *D. ashlandi*, *D. sicilis*, and *Daphnia galeata mendotae* were inversely correlated with the 0 to 10  $\mu$ m size class, which we interpret as a grazing effect on phytoplankton size structure, and positively correlated with an increase in abundance of the > 70  $\mu$ m size class of phytoplankton. CCA suggested that top-down and bottom-up effects were affecting phytoplankton size composition and abundance simultaneously.

**INDEX WORDS:** Lake Michigan, phytoplankton, trophic interactions, food web, zooplankton.

### INTRODUCTION

Considerable variability of the zooplankton community of Lake Michigan has occurred over the

past 40 years. Between 1954 and 1966, the zooplankton community of Lake Michigan underwent striking size-related changes (Wells 1970). Species that declined sharply were the largest cladocerans, calanoid copepods and cyclopoid copepods.

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Medium-sized or small species increased in number, probably in response to selective alewife predation on the larger organisms. After the alewife dieback in 1967 and by 1968, composition of the zooplankton community shifted back toward one similar to 1954 with the exception of *Daphnia galeata mendotae* and *Mesocyclops edax*, which remained rare (Wells 1970).

For the 10-year period starting with 1983, three loosely defined periods of differing zooplankton composition have been suggested: 1983–1986, 1987–1990, and 1990–1992 (Makarewicz et al. 1995). The large cladocerans, calanoid and cyclopoid copepods, which were observed by Wells (1970) to have decreased sharply in Lake Michigan between 1954 and 1966, were by 1983–86 at densities similar to or greater than those in 1954 (Makarewicz et al. 1995). In addition, a new large herbivorous cladoceran *Daphnia pulicaria* had become well established in the offshore waters by 1983. The resurgence of larger zooplankton in Lake Michigan in the early 1980s to abundances reminiscent of those in 1954 was correlated with the sharp decline in the abundance of the planktivorous alewife in 1982 and 1983 (Jude and Tesar 1985, Scavia et al. 1986). In 1986 *Bythotrephes cederstroemi*, a large, exotic, predatory cladoceran species, invaded Lake Michigan.

During the 1987–1990 period, subsequent to the establishment of *B. cederstroemi* in 1986, the relatively large herbivorous Cladocera (*Daphnia pulicaria*, *D. retrocurva*, *Leptodora kindtii*, *Holopedium gibberum*) and the large cyclopoid *Mesocyclops edax* decreased, abundance of the small Cladocera *Bosmina longirostris* was variable but increased, and the mean length of the Cladocera community dropped sharply from 1.5 mm to less than 0.5 mm in 1 year from 1986 to 1987 suggesting the resurgence of a size-selective predator. Lehman (1991) and Lehman and Caceres (1993) suggested that the daphnid composition in the 1985 to 1987 period was consistent with invertebrate predation from *Bythotrephes*, rather than with vertebrate predation. Sprules et al. (1990) argued that since the abundance of *Bosmina* increased and that of *Daphnia* decreased while *Bythotrephes* abundance increased, predation by planktivorous fish was likely rather than by an invertebrate such as *Bythotrephes*. Not all large zooplankton species were reduced in number after 1987, however. The large calanoid *Epischura lacustris* generally increased in abundance, and the abundance of the relatively large *Di-*

*aptomus minutus*, *D. sicilis*, and *D. ashlandi* was greater than those reported for 1954.

By the beginning of the 1990–1992 period, further changes were evident. Populations of the predaceous zooplankton, such as the cladoceran *Leptodora* and the cyclopoid *Mesocyclops edax*, were not observed in the pelagic region of Lake Michigan (Makarewicz et al. 1995). Abundance of the smaller herbivorous Cladocera (*Bosmina longirostris* and *Eubosmina coregoni*) were variable through the 1980s, but they, too, sharply declined during 1991 and 1992. Species diversity and evenness of the cladoceran community in the early 1990s were unlike anything that had been previously reported for Lake Michigan. While there were 10 species of cladocerans in 1985, there were only three by 1991. In 1992 a single species (*D. galeata mendotae*) accounted for over 95% of Cladocera abundance (Makarewicz et al. 1995). Most of the herbivorous copepod species that were present during 1983 to 1985 remained abundant during 1991 and 1992.

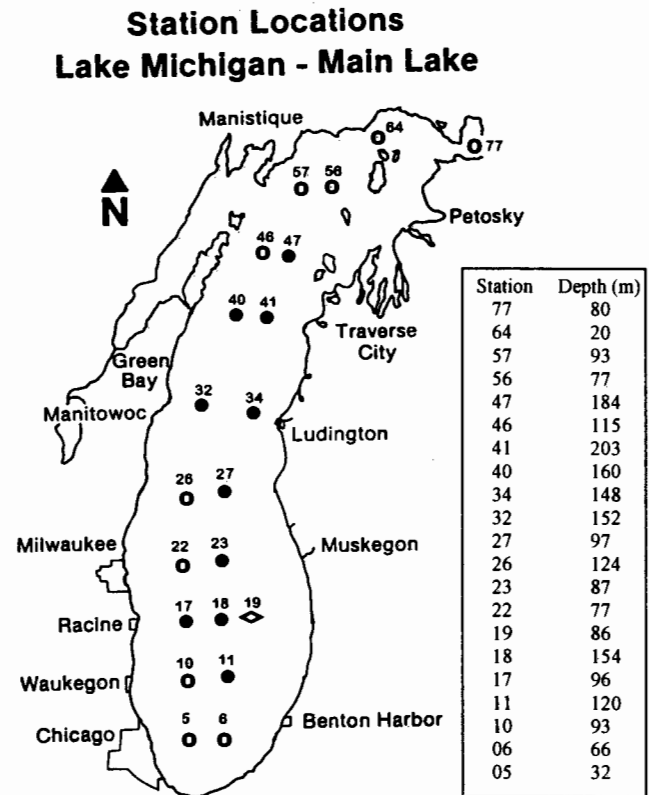
The variability in the zooplankton community over the past 40 years was often associated with periods of shifting composition of the fish community or with the introduction of exotic predatory zooplankton (e.g., Wells 1970, Jude and Tesar 1985, Evans and Jude 1986, Scavia et al. 1986, Stewart and Ibarra 1991, Evans 1992). Furthermore, correlational analysis suggested that alewife, bloater chubs, and the zooplankter *Bythotrephes* were affecting size and biomass of larger species of zooplankton during the 1982 to 1993 period (Makarewicz et al. 1995). Induced by size-selective feeding of fish and predaceous invertebrates, the major changes in the zooplankton community observed over the 10-year period of 1983 to 1992 suggested that some impact should occur on the phytoplankton community if the system were driven by a top-down effect. Unlike Lehman (1988), who looked for impact on chlorophyll levels between 1985 and 1987 and found none despite changes in the herbivorous zooplankton community, this study examined the impact on phytoplankton size class and species composition. With such major changes in the zooplankton community it seemed reasonable to expect that there been changes in phytoplankton species and size composition. Changes, if any, in the relative abundance of phytoplankton size classes were examined to determine if they correlated with either the top-down mediated changes observed in the zooplankton community during the 1980s and 1990s or with any

bottom-up variability in nutrient chemistry. The water quality of the offshore region of Lake Michigan was evaluated to determine if there has been any change during the study period. By considering phytoplankton species composition and size composition, nutrient chemistry, and zooplankton abundance obtained simultaneously over a 10-year period, some insight into these issues was obtained using canonical correspondence analysis.

## METHODS

Phytoplankton, zooplankton, and water chemistry samples were simultaneously collected at each station during 48 cruises during the spring, summer, and autumn from 1983 to 1992. Sampling schedules, station locations, and protocols were selected and implemented to provide information most useful for the evaluation of long-term trends in pelagic water quality and to assess attainment of general and specific objectives of the Great Lakes Water Quality Agreement (GLWQA). The field sampling design was conducted according to the Lake Michigan Surveillance Plan (LMSP) of the Great Lakes International Surveillance Plan (IJC 1986) and the Lake Michigan Implementation Plan contained therein. The LMSP was prepared by the Lake Michigan Task Force for the Water Quality Board of the Great Lakes Regional Office of the International Joint Commission. Prior to implementation of the sampling scheme, draft versions were distributed for external peer review to ensure their scientific integrity and their ability to meet the monitoring requirements of the 1978 Great Lakes Water Quality Agreement (GLWQA 1978, 1987) between the United States and Canada. In 1996 the U.S. Environmental Protection Agency sought another external review of the sampling design. The participants confirmed that the design was appropriate for assessing year-to-year variations and long-term trends in the plankton communities.

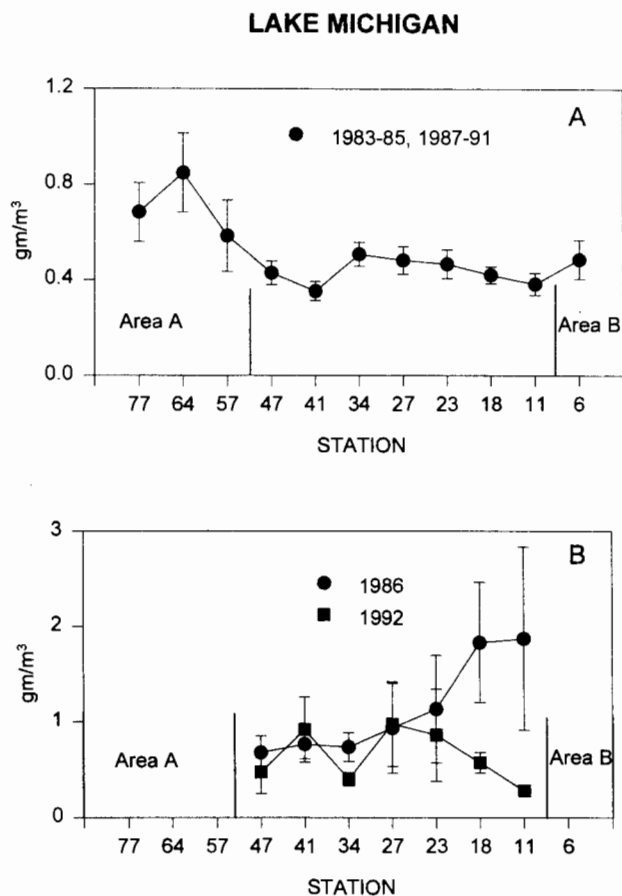
West or east stations were sampled (e.g., 5 or 6, 10 or 11; Fig. 1) on alternate cruises in 1983 and 1984 by sampling the west side of the lake and on the next cruise sampling the east of the lake. This selection of sites was based on previous work which indicated that adjacent east-west sites were within homogenous areas of Lake Michigan. After 1984, stations 5, 6, 10, 22, 26, 46, 57, 56, 64, and 77 were dropped from the sampling scheme. Beginning in 1985, station 19 was added to a network of 11 fixed stations that were sampled on each survey. In this report, to allow north to south comparisons,



**FIG. 1.** Lake Michigan sampling stations, 1983–1992. ○ = sampled only in 1983 and 1984. ● = sampled 1983–1992. ◇ = sampled 1985–1992.

data from stations on an east to west axis were averaged to give one point. For example, data from stations 22 and 23 were averaged to form one point on a north to south transect reported as station 23 in Figures 2 and 3.

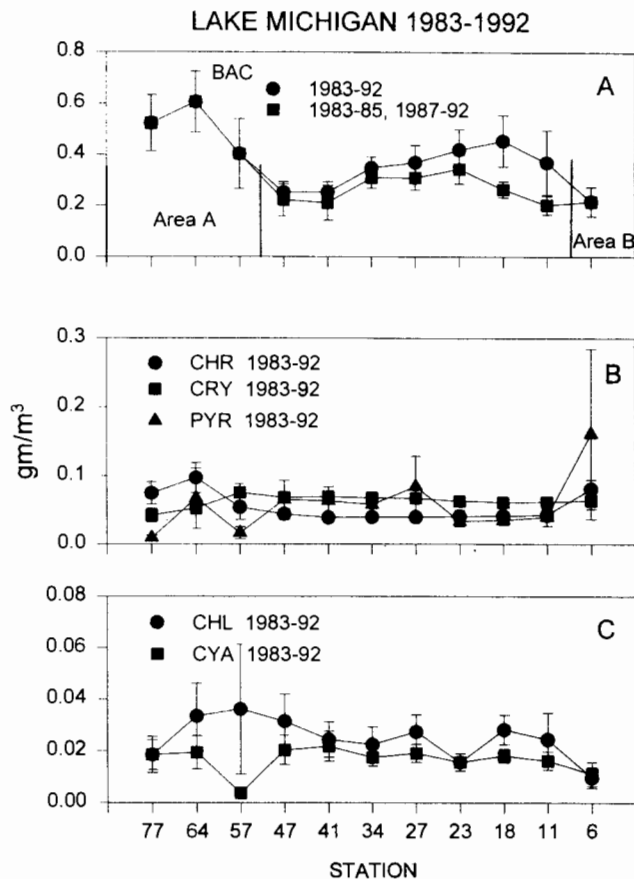
Reported are data from 37 cruises each from the unstratified period (23 March to 7 May) and the stratified summer period (August) (Table 1 in Makarewicz *et al.* 1995). An 8-L PVC Niskin bottle mounted on a General Oceanics™ Rosette sampler with a Guildline™ electrobathythermograph (EBT) was used to collect phytoplankton. Phytoplankton samples were obtained by compositing equal aliquots of samples collected at depths of 1, 5, 10, and 20 m. Since the deep chlorophyll layer does not form until thermal stratification occurs and is at a depth of 40–70 m in August (Fahnenstiel and Scavia 1987a), the species data represented only summer epilimnetic forms and early spring isothermal forms. One-liter samples were immediately preserved with 10 mL of Lugol's solution. When



**FIG. 2.** (A). Geographical distribution of algal biomass in Lake Michigan. Values are the mean for 1983–85, 1987–1991  $\pm$  S.E. (B). Geographical distribution of algal biomass in Lake Michigan, 1986 and 1992. Areas A and B were sampled only in 1983 and 1984.

samples arrived in the laboratory, 10 mL of formalin was added.

All phytoplankton enumeration and identifications were performed by the Bionetics Corporation (1983 to 88), ASci Corp. (1989 and 1990), and Enviroscience (1991 and 92). The settling chamber procedure (Utermöhl 1958) was used to identify (except for diatoms) and enumerate phytoplankton at a magnification of 500x. Each cell in a filament or colony was counted as an individual organism. A second identification and enumeration of diatoms at 1250x was performed after the organic portion was oxidized with 30%  $H_2O_2$  and  $HNO_3$ . The cleaned diatom concentrate was air dried on a #1 cover slip and mounted on a slide (75  $\times$  25 mm) with HYRAX<sup>TM</sup> mounting medium. Replicate identifica-



**FIG. 3.** Geographical distribution of algal biomass in Lake Michigan. Values are the mean  $\pm$  S.E. Areas A and B were sampled in 1983 and 1984 only. BAC = Bacillariophyta, CHR = Chrysophyta, CRY = Cryptophyta, PYR = Pyrrophyta, CHL = Chlorophyta, CYA = Cyanophyta.

tions and counts were made by different analysts on every 10th sample to determine enumeration precision within a division of phytoplankton and to establish consistency of identification. Analytical precision goals for enumerators were based on the Relative Percent Deviation ( $RPD = ((\text{larger count} - \text{smaller count}) / \text{average}) \times 100$ ) (Csuros 1994, ARCS 1994). For example, the precision goal for replicated Bacillariophyta counts was  $\pm 15\%$ . Values outside this goal were rejected and the samples recounted unless a clear explanation was available; e.g., very low abundance of forms in any one division. In addition, validation of species identifications between different enumerators over the 10-year period was made to ensure consistency in nomenclature by recounts of old samples by new

counters. Unidentified rod or spherical shaped Cyanobacteria with a size less than 2  $\mu\text{m}$  (unicells or individuals within a colony) were classified as picoplankton.

The cell volume of each species was computed by applying average dimensions for each species from each sampling station and date to the geometrical shape that most closely resembled the species form, e.g., sphere, cylinder, prolate spheroid, etc. At least 10 specimens of each species were measured from each sample for the cell volume calculation. When fewer than 10 specimens were present, they were measured as they occurred. For most organisms, the measurements were taken from the outside wall to outside wall. The dimensions of the protoplast were measured for loricated forms, while the dimensions of individual cells were measured for filaments and colonial forms. Biovolume was converted to biomass assuming a specific gravity of 1.0 for all phytoplankton ( $\text{mm}^3/\text{L} = \text{g}/\text{m}^3$ ) (Willen 1959, Nauwerck 1963).

Methodology for zooplankton collection and enumeration may be found in Makarewicz *et al.* (1995). Water chemistry analysis generally followed "Methods for Chemical Analysis of Water and Wastes" (USEPA 1979). In addition, the following modifications or methods were employed for total kjeldahl nitrogen (Jirka *et al.* 1976, Technicon Method #154-71W), total phosphorus (Technicon Method #155-79-02), nitrate/nitrite (Technicon Method #100-70W), dissolved reactive silica (Technicon Method #105-71W, APHA (1992): Method 4500-Si F). All Technicon Methods refer to Technicon Industrial Systems, Tarrytown, NY.

### Data Analysis

To analyze the data for causes of variability in phytoplankton size classes as percent abundance, we chose canonical correspondence analysis (CCA) over multiple regression. In multiple regression, separate analyses are required for each size class, which cannot be combined easily to get an overview of how community composition varies with the environment (ter Brake 1986). To prevent the influence of a few high abundance values from unduly influencing the analysis, the zooplankton data were transformed by taking logarithms [ $\log_{10}(\text{abundance})$ ] (ter Brake 1986). Species data were presented as percent abundance of four size classes: ultraplankton (0 to 10  $\mu\text{m}$ ), small nanoplankton (10 to 20  $\mu\text{m}$ ), large nanoplankton (20 to 70  $\mu\text{m}$ ) and net plankton (> 70  $\mu\text{m}$ ) (Mills 1975,

Strickland 1960). All data used in CCA represented a separate spring and summer average for all stations within a given year. Although the zooplankton data consisted of over 40 species and the water chemistry included over 26 analytes, the CCA analysis was limited to nine environmental variables because only 10 years of data were available for each seasonal analysis. Environmental variables chosen were the most abundant species of crustacean zooplankton in the spring or summer [summer: *Daphnia retrocurva*, *Daphnia pulicaria*, *Daphnia galeata mendotae*, *Bosmina longirostris*, *Diaptomus minutus*, and *D. ashlandi*; spring: *D. minutus*, *D. ashlandi*, *D. sicilis*, and *Limnocalanus macrurus*] and physical/chemical factors (summer: silica, total phosphorus, and the N/P ratio [nitrate nitrogen + total kjeldahl nitrogen : total phosphorus by weight]; spring: total phosphorus, silica, nitrate, N:P, and temperature) generally known to affect phytoplankton biomass.

Statistical evaluations and other data manipulations were conducted in Minitab and the INFO data management system (Henco Software, Inc.), while the ordination and Monte Carlo test was done in the Windows version of PC-ORD (MJM Software, Inc.). For the CCA, a Monte Carlo Test was performed (number of randomizations = 99) testing the null hypothesis that no relationship existed between matrices at  $P < 0.01$ . Generally, significant differences ( $P < 0.05$ ) were determined by one-way analysis of variance and Tukey's Honestly Significant Difference (HSD) test (Dowdy and Wearden 1983).

## RESULTS

### Annual Abundance of Major Algal Groups

From 1983 to 1992, 543 species representing 145 genera comprised the offshore phytoplankton community of Lake Michigan. Over 10 years, 39 common species and varieties accounted for 96.0% of the total abundance and 85.6% of the total biomass over the 10-year period (Table 1).

For the 10-year spring and summer period, the algal divisions/groups with the highest average cell abundance were the picoplankton (13,411 cells/mL), Cyanophyta (3,199 cells/mL), and the Chrysophyta (839 cells/mL) (Table 2). The Cyanophyta increased from 3.8% of the phytoplankton abundance in the 1983 to 1987 period to 36.8% of the phytoplankton abundance in the 1988 to 1992 period while the Chrysophyta and picoplankton decreased in abundance for the

**TABLE 1.** Summary of common phytoplankton species occurrence in Lake Michigan during 1983–1992. Summary includes the average population density and biovolume, and the relative abundance (% of total cells and % of total biovolume). Common species were arbitrarily defined as having an abundance  $\geq 0.5\%$  of the total cells or  $\geq 0.5\%$  of the total biovolume.

Taxon	Average Cells/mL	% of Total Cells	Mean Biovolume	% of Total Biovolume $\mu\text{m}^3/\text{mL}$
<b>BACILLARIOPHYTA</b>				
<i>Asterionella formosa</i>	17.6	0.10	7,889	1.47
<i>Aulacoseira islandica</i>	27.7	0.15	34,216	6.36
<i>Aulacoseira italica</i>	31.3	0.17	8,492	1.58
<i>Cyclotella comta</i>	3.3	0.02	7,984	1.48
<i>Cymatopleura solea</i>	0.1	0.00	3,521	0.65
<i>Fragilaria crotonensis</i>	26.6	0.15	18,058	3.36
<i>Nitzschia lauenburgiana</i>	0.5	0.00	3,358	0.62
<i>Rhizosolenia eriensis</i>	4.6	0.03	26,070	4.84
<i>Rhizosolenia longiseta</i>	10.4	0.06	11,178	2.08
<i>Stephanodiscus alpinus</i>	10.4	0.06	83,256	15.47
<i>Stephanodiscus niagarae</i>	1.9	0.01	38,223	7.10
<i>Stephanodiscus transilvanicus</i>	5.0	0.03	55,418	10.30
<i>Synedra ulna</i>	0.6	0.00	4,863	0.90
<i>Tabellaria flocculosa</i>	8.7	0.05	23,669	4.40
		0.81		60.61
<b>CHLOROPHYTA</b>				
<i>Cosmarium</i> sp.	0.4	0.00	2,993	0.56
Green coccoid	82.4	0.45	5,446	1.01
		0.45		1.57
<b>CHRYSTOPHYTA</b>				
<i>Chromulina</i> sp.	196.4	1.07	5,767	1.07
<i>Dinobryon divergens</i>	18.4	0.10	3,905	0.73
<i>Dinobryon sociale</i>	27.5	0.15	3,422	0.64
<i>Haptophyceae</i>	168.2	0.92	3,479	0.65
<i>Ochromonas</i> sp.	318.0	1.74	12,606	2.34
		3.98		5.42
<b>CRYPTOPHYTA</b>				
<i>Cryptomonas erosa</i>	11.2	0.06	24,496	4.55
<i>Cryptomonas marssonii</i>	4.3	0.02	4,482	0.83
<i>Cryptomonas phaseolus</i>	6.4	0.04	2,889	0.54
<i>Rhodomonas minuta</i>	191.8	1.05	16,571	3.08
		1.17		9.00
<b>CYANOPHYTA</b>				
<i>Agmenellum quadruplicatum</i>	243.2	1.33	404	0.08
<i>Anacystis incerta</i>	1,035.4	5.66	425	0.08
<i>Anacystis montana</i>	428.0	2.34	4,478	0.83
<i>Aphanocapsa delicatissima</i>	94.1	0.51	14	0.00
<i>Aphanothece clathrata</i>	813.7	4.45	236	0.04
<i>Coelosphaerium naegelianum</i>	99.7	0.55	1,384	0.26
<i>Microcystis elachista</i>	131.7	0.72	374	0.07
<i>Oscillatoria limnetica</i>	122.7	0.67	1,117	0.21
		16.23		1.57
<b>PICOPLANKTON</b>				
rods	2,391.0	13.07	4,561	0.85
spheres	10,792.6	59.01	3,945	0.73
spherical—flagellates	227.0	1.24	267	0.05
		73.32		1.63

Continued

TABLE 1. Continued.

Taxon	Average Cells/mL	% of Total Cells	Mean Biovolume	% of Total Biovolume $\mu\text{m}^3/\text{mL}$
<b>PYRROPHYTA</b>				
<i>Ceratium hirundinella</i>	0.4	0.00	15,987	2.97
<i>Gymnodinium</i> sp.	2.3	0.01	6,543	1.22
<i>Peridinium</i> sp.	1.8	0.01	8,430	1.57
		0.02		5.75
		96.00		85.55

same two time periods (Table 2). The Bacillariophyta contained the largest number of species (220 – > 40% of all taxa identified) and by far the highest relative biomass for the study period (mean = 64.1%, range = 13.8% to 84.4% of the total, Table 3). The number of species of Chlorophyta was also high (133 – 24% of all taxa identified), but the relative biomass was much lower (mean = 4.7%). In contrast, few Pyrrophyta species were present (11), but their relative biomass (mean = 6.3%) was similar to that of the Chlorophyta (Table 3).

Time-trend patterns in relative biomass of algal divisions from 1983 through 1992 did not emerge from the data. Except for 1989, when the relative biomass of diatoms was unusually low (13.8%), relative biomass of diatoms dominated that of the other algal divisions ranging from 48.2% to 84.4%, with no distinct upward or downward trend. In 1989, when diatom biomass was low, the relative and absolute biomass (Table 3) of the Cyanophyta, Chlorophyta, Chrysophyta, and Cryptophyta were greater than in previous and subsequent years. During the summer of 1989, abundance of diatoms was the second lowest recorded, while summer abundance of Chlorophyta was the highest over the 1983 to 92 period (Table 4).

#### Geographical Abundance and Distribution of Major Algal Groups

Usually, mean algal biomass was high in northern Lake Michigan, decreased to a minimum at station 41 (Fig. 2A), increased to station 34 and then decreased southerly in Lake Michigan until station 11. Biomass then increased slightly again at station 6. This geographical pattern was determined by the diatoms (Fig. 3A). Pyrrophyta, Chrysophyta, and Cryptophyta biomass were generally similar from north to south with the exception of the shallower

station 6 and the shallower or nearshore northern stations (77, 64, 57) (Fig. 3B). At these shallower/nearshore stations, Chrysophyta biomass was higher. Pyrrophyta biomass was also higher at station 6 but generally more variable at stations 77, 64, and 57. Chlorophyta and Cyanophyta biomass varied little in the pelagic region of the lake but appeared lower at the southern station 6 (Fig. 3C). Chlorophyta and Cyanophyta biomass was also lower at the northern stations 77 and 57, respectively.

In 1986, phytoplankton biomass increased from north to south (Fig. 2B) due to a bloom of *Stephanodiscus alpinus* and *S. transilvanicus* in southern Lake Michigan. The higher abundance in 1992 at stations 41, 27, and 23 were also due to blooms of *Stephanodiscus alpinus*, *S. transilvanicus*, and *Aulacoseira islandica*. The far northern stations (stations 57, 56, 64, and 77) and the most southern stations (stations 5 and 6), areas A and B in Figures 2 and 3, were sampled only in 1983 and 1984.

#### Dominant and Indicator Species (1983–92)

An unidentified green coccoid (Chlorophyta), *Ochromonas* sp. and *Chromulina* sp. (Chrysophyta), *Rhodomonas minuta* (Cryptophyta), *Anacystis montana* and *Oscillatoria limnetica* (Cyanophyta) were the numerically dominant non-diatoms in their respective divisions during the 1983–87 period (Table 5). For the 1988–92 period, a similar group of non-diatoms was numerically dominant with the exception of the Haptophyceae (Chrysophyta), *Anacystis incerta* and *Aphanothece clathrata* (Cyanophyta) (Table 6), which were more prevalent than during the 1983–87 period. *Ochromonas* sp. and *Chromulina* sp. decreased in abundance from 1983–87 to the 1988–92 period.

Of the dominant Chrysophyta, Cryptophyta and

**TABLE 2.** Time trends in phytoplankton abundance (1983 to 1992). Only major divisions from the spring and summer (August) are considered. BAC = Bacillariophyta, CHL = Chlorophyta, CHR = Chrysophyta, CRY = Cryptophyta, CYA = Cyanophyta, PYR = Pyrrophyta, PICO = Picoplankton. The averages for the 83–87, 88–92, and 83–92 periods are weighted means that consider the number of stations in each year. Values in parentheses are percent of total.

	ABUNDANCE (Cells/mL)								Mean Abundance
	BAC	CHL	CHR	CRY	CYA	PYR	PICO	OTHER	
1983	240	153	1,156	307	390	3.8	19,228	39	21,517
1984	516	158	1,923	347	921	4.7	20,727	40	24,637
1985	252	205	1,359	328	1,134	6.0	18,544	41	21,869
1986	326	326	604	298	478	4.5	13,321	107	15,464
1987	161	158	248	176	448	3.2	3,908	30	5,132
1988	319	314	468	244	1,875	8.3	10,730	20	13,978
1989	115	661	640	253	15,902	6.7	22,176	26	39,780
1990	198	142	387	236	5,987	7.0	5,888	22	12,867
1991	205	115	233	231	4,651	5.2	2,790	15	8,245
1992	318	168	365	374	4,903	5.9	7,549	23	13,706
Mean (83–87)	315 (1.7)	201 (1.1)	1160 (6.1)	302 (1.6)	718 (3.8)	4.6 (.02)	16,213 (85.5)	56 (.3)	18,970
Mean (88–92)	229 (1.3)	281 (1.6)	423 (2.4)	257 (1.5)	6,406 (36.8)	6.8 (.04)	9,785 (56.2)	22 (.1)	17,410
Mean (83–92)	278 (1.5)	236 (1.3)	839 (4.6)	283 (1.5)	3,199 (17.5)	5.5 (.03)	13,411 (73.3)	39 (.2)	18,291

**TABLE 3.** Time trends in phytoplankton biomass (1983 to 1992). Only major divisions from the spring and summer (August dates only) are considered. BAC = Bacillariophyta, CHL = Chlorophyta, CHR = Chrysophyta, CRY = Cryptophyta, CYA = Cyanophyta, PYR = Pyrrophyta, PICO = Picoplankton. Values in parentheses are percent of total. The averages for the 83–87, 88–92, and 83–92 periods are weighted means that consider the number of stations in each year.

	BAC	CHL	CHR	CRY	CYA	PYR	PICO	OTHER	Mean Biomass
	g/m <sup>3</sup> %	g/m <sup>3</sup> %	g/m <sup>3</sup> %	g/m <sup>3</sup> %	g/m <sup>3</sup> %	g/m <sup>3</sup> %	g/m <sup>3</sup> %	g/m <sup>3</sup> %	g/m
1983	.199 (52.6)	.023 (6.1)	.042 (11.1)	.048 (12.7)	.013 (3.4)	.042 (11.3)	.008 (2.1)	.002 (0.5)	.377
1984	.361 (69.7)	.013 (2.4)	.048 (9.3)	.065 (12.5)	.012 (2.3)	.009 (1.8)	.009 (1.7)	.001 (0.2)	.518
1985	.340 (63.3)	.011 (2.0)	.050 (9.3)	.086 (16.0)	.017 (3.2)	.024 (4.5)	.008 (1.4)	.001 (0.2)	.537
1986	1.02 (84.4)	.042 (3.5)	.035 (2.9)	.055 (4.5)	.013 (1.1)	.022 (1.8)	.019 (1.6)	.004 (0.3)	1.21
1987	.187 (69.5)	.010 (3.8)	.010 (3.9)	.036 (13.5)	.006 (2.2)	.016 (6.0)	.002 (0.7)	.002 (0.7)	.269
1988	.235 (58.7)	.020 (5.0)	.025 (6.4)	.047 (11.7)	.011 (2.7)	.052 (12.9)	.009 (2.3)	.001 (0.3)	.400
1989	.060 (13.8)	.097 (22.4)	.084 (19.4)	.089 (20.4)	.047 (10.9)	.037 (8.5)	.018 (4.1)	.002 (0.5)	.434
1990	.235 (48.2)	.023 (4.6)	.043 (8.7)	.084 (17.3)	.039 (8.1)	.055 (11.2)	.006 (1.1)	.002 (0.4)	.487
1991	.315 (72.5)	.009 (2.2)	.017 (3.9)	.045 (10.3)	.018 (4.2)	.028 (6.4)	.002 (0.4)	.000 (0.0)	.434
1992	.401 (62.4)	.014 (2.2)	.030 (4.7)	.091 (14.1)	.027 (4.3)	.073 (11.4)	.005 (0.8)	.001 (0.2)	.642
Mean (83–87)	.428 (72.0)	.020 (3.3)	.040 (6.7)	.061 (10.2)	.013 (2.1)	.023 (3.8)	.009 (1.6)	.001 (0.2)	.595
Mean (88–92)	.238 (51.2)	.032 (7.0)	.040 (8.5)	.069 (14.9)	.028 (6.1)	.048 (10.3)	.008 (1.7)	.002 (0.4)	.465
Mean (83–92)	.345 (64.1)	.025 (4.7)	.040 (7.4)	.064 (12.0)	.019 (3.6)	.034 (6.3)	.009 (1.6)	.002 (0.4)	.538



**TABLE 4.** Lake Michigan mean spring and summer (August dates) division abundances (cells/mL) 1983–1992.

Year	Bacillariophyta		Chlorophyta		Chrysophyta		Cyanophyta		Pyrrophyta		Cryptophyta		Picoplankton	
	Spring (cells/ mL)	Summer (cells/ mL)	Spring (cells/ mL)	Summer (cells/ mL)	Spring (cells/ mL)	Summer (cells/ mL)	Spring (cells/ mL)	Summer (cells/ mL)	Spring (cells/ mL)	Summer (cells/ mL)	Spring (cells/ mL)	Summer (cells/ mL)	Spring (cells/ mL)	Summer (cells/ mL)
1983	331	149	165	141	683	1,630	419	362	3.9	3.7	356	258	15,927	22,528
1984	427	575	102	195	930	2,585	918	922	3.5	5.5	237	420	10,078	27,814
1985	380	60	187	233	1,022	1,866	396	2,241	3.5	9.7	303	365	11,157	29,624
1986	564	88	195	457	335	873	164	792	5.1	3.8	309	288	4,944	21,699
1987	180	122	77	330	108	542	318	720	1.6	6.6	134	265	1,131	9,740
1988	462	182	76	542	211	714	566	3,126	7.0	9.5	230	256	2,853	18,264
1989	174	86	417	784	299	811	1,927	22,889	4.3	8.0	333	213	18,879	23,825
1990	174	222	40	243	193	582	1,652	10,321	5.5	8.5	173	299	6,348	5,427
1991	239	137	46	253	187	325	1,042	11,870	6.0	3.6	212	268	2,052	4,267
1992	396	240	121	216	215	515	1,663	8,142	5.4	6.4	244	504	3,211	11,888

TABLE 5. Summary of common phytoplankton species occurrence in Lake Michigan during 1983 - 1987. Summary includes the average population density and biovolume, and the relative abundance (% of total cells and % of total biovolume). Common species were arbitrarily defined as having an abundance  $\geq 0.5\%$  of the total cells or  $\geq 0.5\%$  of the total biovolume.

Taxon	Average Cells/mL	% of Total Cells	Mean Biovolume	% of Total Biovolume $\mu\text{m}^3/\text{mL}$
<b>BACILLARIOPHYTA</b>				
<i>Asterionella formosa</i>	15.9	0.08	5,300	0.89
<i>Aulacoseira islandica</i>	29.5	0.16	29,692	4.99
<i>Aulacoseira italica</i>	34.9	0.18	7,230	1.22
<i>Cyclotella comta</i>	3.7	0.02	7,796	1.31
<i>Cymatopleura solea</i>	0.2	0.00	5,656	0.95
<i>Fragilaria crotonensis</i>	27.4	0.14	18,535	3.12
<i>Nitzschia lauenburgiana</i>	0.7	0.00	4,573	0.77
<i>Rhizosolenia eriensis</i>	5.5	0.03	35,833	6.02
<i>Rhizosolenia longiseta</i>	17.8	0.09	19,240	3.23
<i>Stephanodiscus alpinus</i>	13.3	0.07	112,012	18.83
<i>Stephanodiscus niagarae</i>	2.3	0.01	48,778	8.20
<i>Stephanodiscus transilvanicus</i>	4.0	0.02	72,097	12.12
<i>Synedra ulna</i>	1.0	0.01	8,186	1.38
<i>Tabellaria flocculosa</i>	11.3	0.06	30,186	5.07
		0.88		68.09
<b>CHLOROPHYTA</b>				
<i>Cosmarium</i> sp.	0.5	0.00	4,183	0.70
Green coccoid	54.9	0.29	3,076	0.52
		0.29		1.22
<b>CHRYSTOPHYTA</b>				
<i>Chromulina</i> sp.	327.4	1.73	6,958	1.17
<i>Dinobryon divergens</i>	18.4	0.10	3,394	0.57
<i>Dinobryon sociale</i>	35.1	0.19	4,351	0.73
<i>Haptophyceae</i>	142.3	0.75	2,295	0.39
<i>Ochromonas</i> sp.	512.1	2.70	14,732	2.48
		5.46		5.33
<b>CRYPTOPHYTA</b>				
<i>Cryptomonas erosa</i>	10.4	0.06	23,317	3.92
<i>Cryptomonas marssonii</i>	2.8	0.01	3,198	0.54
<i>Rhodomonas minuta</i>	199.9	1.05	17,518	2.94
		1.12		7.40
<b>CYANOPHYTA</b>				
<i>Anacystis montana</i>	284.5	1.50	2,376	0.40
<i>Coelosphaerium naegelianum</i>	107.1	0.56	723	0.12
<i>Oscillatoria limnetica</i>	175.1	0.92	1,472	0.25
		2.99		0.77
<b>PICOPLANKTON</b>				
rods	1,457.1	7.68	3,243	0.55
spheres	14,355.9	75.68	5,671	0.95
spherical— flagellates	400.1	2.11	472	0.08
		85.47		1.58
<b>PYRRROPHYTA</b>				
<i>Ceratium hirundinella</i>	0.3	0.00	10,189	1.71
<i>Gymnodinium</i> sp.	1.8	0.01	6,405	1.08
<i>Peridinium</i> sp.	1.0	0.01	3,765	0.63
		0.02		3.42
		96.23		87.81

Cyanophyta, *Anacystis montana*, *Oscillatoria* spp., and *Rhodomonas minuta* were prevalent, if not dominant, in each year of the 10-year study. *Monoraphidium contortum* was the dominant green alga in 1983 and 1984, but a "Green coccoid" was the numerically dominant green alga from 1985 through 1992 with the exception of 1991 when *Monoraphidium minutum* was the numerical dominant. Of the chrysophytes, *Chromulina* sp. and *Ochromonas* sp. were predominant and *Dinobryon sociale* was prevalent from 1983 through 1985. After 1985, *Chromulina* sp., *Ochromonas* sp., and *D. sociale* became less abundant while the Haptophyceae, predominantly a marine group (Stoermer and Tuchman 1979), became progressively more prevalent in Lake Michigan (Fig. 4).

Numerically dominant diatoms in the 1983–87 period included *Fragilaria crotonensis*, *Aulacoseira italica*, and *A. islandica*. On a biomass basis, *Stephanodiscus alpinus*, *S. transilvanicus*, *S. niagarae*, and *Rhizosolenia eriensis* were predominant (Table 5). A similar group of diatoms was dominant in the 1988–1992 period (Table 6). The dominance (biomass basis) of the various species of *Stephanodiscus* over the 1983–87 period was due to the unusually high biomass (over 45% of total biomass) of *S. alpinus* and *S. transilvanicus* in 1986 and 1987 (Table 7).

The 5-year averages presented in Tables 5 and 6 are misleading by suggesting that dominant species do not vary. In fact, a succession of dominant diatoms over the past 10 years was observed (Table 7). This is particularly noticeable when species are considered on a biomass basis. For example, the dominant diatom on a biomass basis was *Tabellaria flocculosa* in 1983 (16.6% of the total biomass), *Rhizosolenia eriensis* in 1984 (22.2% of the total biomass), *Stephanodiscus niagarae* in 1985 (10.4% of the total biomass), *Stephanodiscus alpinus* in 1986, 1987, and 1991 (35.0%, 42.7% and 20.5% of the total biomass, respectively), *Asterionella formosa* in 1988 (9.8% of the total biomass), *Stephanodiscus transilvanicus* in 1990 (16.0% of the total biomass), and *Aulacoseira islandica* in 1992 (21.7% of the total biomass). Except for *Stephanodiscus niagarae*, which is a eutrophic indicator species (Stoermer and Yang 1970), all these dominant species are associated with mesotrophic conditions. Thus for the 10-year period: *Fragilaria crotonensis*, *Aulacoseira italica*, and *A. islandica* were numerically prevalent each year. On a biomass basis, various organisms were predominant each year, including *Stephanodiscus alpinus*, *S. transil-*

*vanicus*, *S. niagarae*, *Rhizosolenia eriensis*, *Tabellaria flocculosa*, *Fragilaria crotonensis*, *Asterionella formosa*, and *Aulacoseira islandica*.

These results are similar to those of Fahnenstiel and Scavia (1987b), who sampled during the spring and summer at one offshore site near Grand Haven from 1982 to 84. Their site is near the deeper station 23 (Fig. 1). Dominant diatoms observed by Fahnenstiel and Scavia (1987b) included *Aulacoseira islandica*, *Tabellaria flocculosa* var. *linearis*, *Tabellaria* spp., *Aulacoseira italica* spp. *subartica*, and *Fragilaria crotonensis* with lesser amounts of *Asterionella formosa*. These diatom dominants were similar to the six most prevalent diatoms observed at station 23 in 1983 and 1984 with the following exceptions: *Asterionella formosa* was not a dominant species, *Stephanodiscus alpinus* (1983) and *S. transilvanicus* (1984) were co-dominants in the spring, and *Rhizosolenia eriensis* was prevalent in the summer of 1984 at station 23.

#### Temporal Trends in Phytoplankton Size Distribution

Size distribution and abundance of phytoplankton significantly changed during the spring and summer periods (Figs. 5A and B). Over the 10-year study period during the spring, there was a general downward trend in percent abundance of the 0 to 10  $\mu\text{m}$  size class, interrupted by a peak in 1989 and 1990, from approximately 90% to 68% of the total phytoplankton abundance. During the same period, cells of the > 70  $\mu\text{m}$  size class (filaments, colonial algae, and large unicell algae) increased to over 21.9% of the phytoplankton abundance by 1991 (Fig. 5A).

During the summer, relative abundance of the 0 to 10  $\mu\text{m}$  size class remained stable around 95% of the total phytoplankton abundance from 1983 to 1987, decreased to 41.8% in 1990 and increased slightly by 1992 (Fig. 5B). Percent abundance of the > 70  $\mu\text{m}$  size class was the inverse of the 0 to 10  $\mu\text{m}$  size class (Fig. 5B).

#### Water Chemistry

There were no trends in spring and summer temperature, total phosphorus and nitrate levels or summer silica levels from 1983 to 1992. However, spring silica concentrations increased significantly while summer N:P ratios decreased significantly (Table 8).

**TABLE 6.** Summary of common phytoplankton species occurrence in Lake Michigan during 1988 – 1992. Summary includes the average population density and biovolume, and the relative abundance (% of total cells and % of total biovolume). Common species were arbitrarily defined as having an abundance  $\geq 0.5\%$  of the total cells or  $\geq 0.5\%$  of the total biovolume.

Taxon	Average Cells/mL	% of Total Cells	Mean Biovolume	% of Total Biovolume $\mu\text{m}^3/\text{mL}$
<b>BACILLARIOPHYTA</b>				
<i>Asterionella formosa</i>	19.9	0.11	11,240	2.42
<i>Aulacoseira islandica</i>	25.4	0.15	40,070	8.62
<i>Aulacoseira italica</i>	26.6	0.15	10,124	2.18
<i>Cyclotella comta</i>	2.8	0.02	8,228	1.77
<i>Fragilaria crotonensis</i>	25.4	0.15	17,441	3.75
<i>Rhizosolenia eriensis</i>	3.3	0.02	13,439	2.89
<i>Stephanodiscus alpinus</i>	6.6	0.04	46,053	9.91
<i>Stephanodiscus niagarae</i>	1.5	0.01	24,569	5.29
<i>Stephanodiscus transilvanicus</i>	6.2	0.04	33,839	7.28
<i>Tabellaria flocculosa</i>	5.3	0.03	15,238	3.28
		0.71		47.40
<b>CHLOROPHYTA</b>				
Green coccoid	118.0	0.68	8,512	1.83
<i>Oocystis gigas</i> v. <i>incrassata</i>	0.8	0.00	3,487	0.75
		0.68		2.58
<b>CHRYSTOPHYTA</b>				
<i>Chromulina</i> sp.	26.9	0.15	4,225	0.91
<i>Dinobryon divergens</i>	18.4	0.11	4,567	0.98
<i>Haptophyceae</i>	201.7	1.16	5,012	1.08
<i>Mallomonas</i> sp.	1.6	0.01	3,287	0.71
<i>Ochromonas</i> sp.	66.9	0.38	9,855	2.12
		1.81		5.80
<b>CRYPTOPHYTA</b>				
<i>Cryptomonas caudata</i>	8.3	0.05	2,971	0.64
<i>Cryptomonas erosa</i>	12.3	0.07	26,022	5.60
<i>Cryptomonas marssonii</i>	6.2	0.04	6,142	1.32
<i>Cryptomonas phaseolus</i>	11.1	0.06	5,578	1.20
<i>Rhodomonas minuta</i>	181.4	1.04	15,346	3.30
		1.26		12.07
<b>CYANOPHYTA</b>				
<i>Agmenellum quadruplicatum</i>	555.7	3.19	925	0.20
<i>Anacystis incerta</i>	2,375.0	13.64	976	0.21
<i>Anacystis montana</i>	613.7	3.53	7,198	1.55
<i>Aphanocapsa delicatissima</i>	215.8	1.24	33	0.01
<i>Aphanothece clathrata</i>	1,866.5	10.72	541	0.12
<i>Coelosphaerium naegelianum</i>	90.2	0.52	2,240	0.48
<i>Microcystis elachista</i>	302.0	1.73	859	0.18
<i>Oscillatoria</i> sp.	88.8	0.51	1,604	0.35
<i>Synechococcus</i> sp.	90.6	0.52	5,076	1.09
		35.60		4.19
<b>PICOPLANKTON</b>				
rods	3,599.3	20.67	6,268	1.35
spheres	6,182.5	35.51	1,712	0.37
		56.19		1.72
<b>PYRROPHYTA</b>				
<i>Ceratium hirundinella</i>	0.5	0.00	23,488	5.06
<i>Gymnodinium helveticum</i>	0.2	0.00	2,566	0.55
<i>Gymnodinium</i> sp.	3.0	0.02	6,722	1.45
<i>Peridinium</i> sp.	2.9	0.02	14,466	3.11
		0.04		10.17
		96.29		83.92

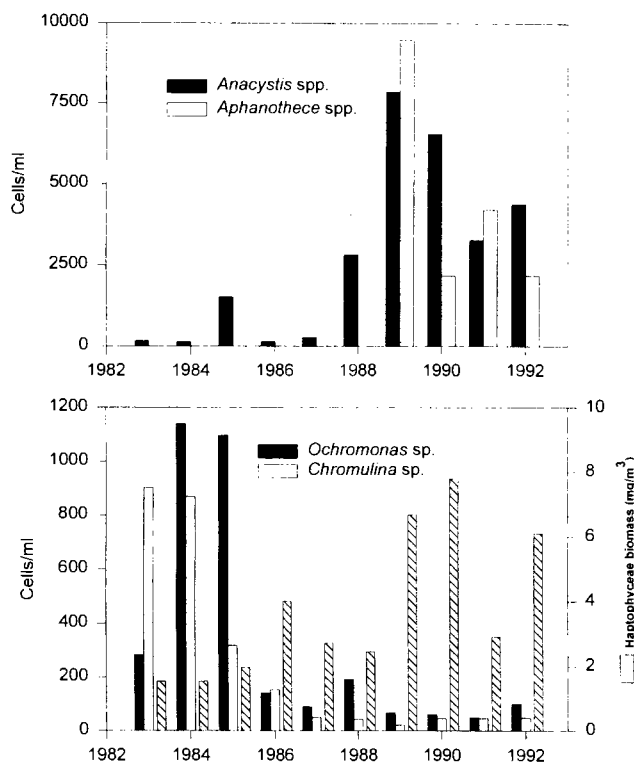


FIG. 4. Mean annual abundance of *Aphanothece*, *Anacystis*, *Chromulina*, *Ochromonas*, and biomass of *Haptophyceae*, 1983–1992.

#### Canonical Correspondence Analysis (CCA)

The influence of the limnological variables on spring phytoplankton size class abundance over the 10-year period were examined using CCA. 88% of

the variability observed in the percent abundance of the phytoplankton size classes from 1983 to 1992 was explained by environmental axis 1, while environmental axes 2 and 3 explained 11.6 and 0.4% of the variability (Fig. 6). The eigenvalue of axes 1 to 3 were fairly low (0.07, 0.01, and 0.00). Because axis 1 explained a high percentage of the variability, axes 2 and 3 were not interpreted further. The 0–10  $\mu\text{m}$ , 10–20  $\mu\text{m}$ , and > 70  $\mu\text{m}$  size classes were strongly correlated with axis 1 (Table 9).

In the summer ordination, 99.2% of the variability observed in the percent abundance of the phytoplankton size classes from 1983 to 1992 was explained by environmental axis 1, while environmental axes 2 and 3 explained only 0.8 and 0.1% of the variability (Fig. 7). The eigenvalue of axis 1 (0.22) versus axis 2 (0.002) and axis 3 (0.000) also suggested the importance of axis 1 in the joint plot. Thus axes 2 and 3 were not interpreted further. The phytoplankton size classes 0–10  $\mu\text{m}$ , 10–20  $\mu\text{m}$ , and > 70  $\mu\text{m}$  were strongly correlated with axis 1 (Table 9). Size class 20–70  $\mu\text{m}$  was poorly correlated with axis 1. Monte Carlo tests of both the spring and summer CCA indicated a significant relationship between the limnological variables and relative abundance for axis 1.

#### DISCUSSION

##### Has the Water Quality of Lake Michigan Improved?

Stoermer and Yang (1970), in a comparison of modern and historic records, reported that taxa characteristic of disturbed situations were rapidly

TABLE 7. Dominant diatom species (biomass basis) from 1983 to 92. Values are percent of total biomass for the year.

Year	Species	% Biomass	Year	Species	% Biomass
1983	<i>Tabellaria flocculosa</i>	16.6	1988	<i>Asterionella formosa</i>	9.8
	<i>Stephanodiscus alpinus</i>	7.9		<i>Stephanodiscus niagarae</i>	9.3
1984	<i>Rhizosolenia eriensis</i>	22.2	1989	<i>Tabellaria flocculosa</i>	2.2
	<i>Fragilaria crotonensis</i>	8.1		<i>Fragilaria crotonensis</i>	1.7
1985	<i>Stephanodiscus niagarae</i>	10.4	1990	<i>Stephanodiscus transilvanicus</i>	16.0
	<i>Aulacoseira islandica</i>	8.9		<i>Rhizosolenia eriensis</i>	8.7
1986	<i>Stephanodiscus alpinus</i>	35.0	1991	<i>Stephanodiscus alpinus</i>	20.5
	<i>Stephanodiscus transilvanicus</i>	25.9		<i>Aulacoseira islandica</i>	19.2
1987	<i>Stephanodiscus alpinus</i>	42.7	1992	<i>Stephanodiscus alpinus</i>	15.2
	<i>Stephanodiscus transilvanicus</i>	4.3		<i>Aulacoseira islandica</i>	21.7

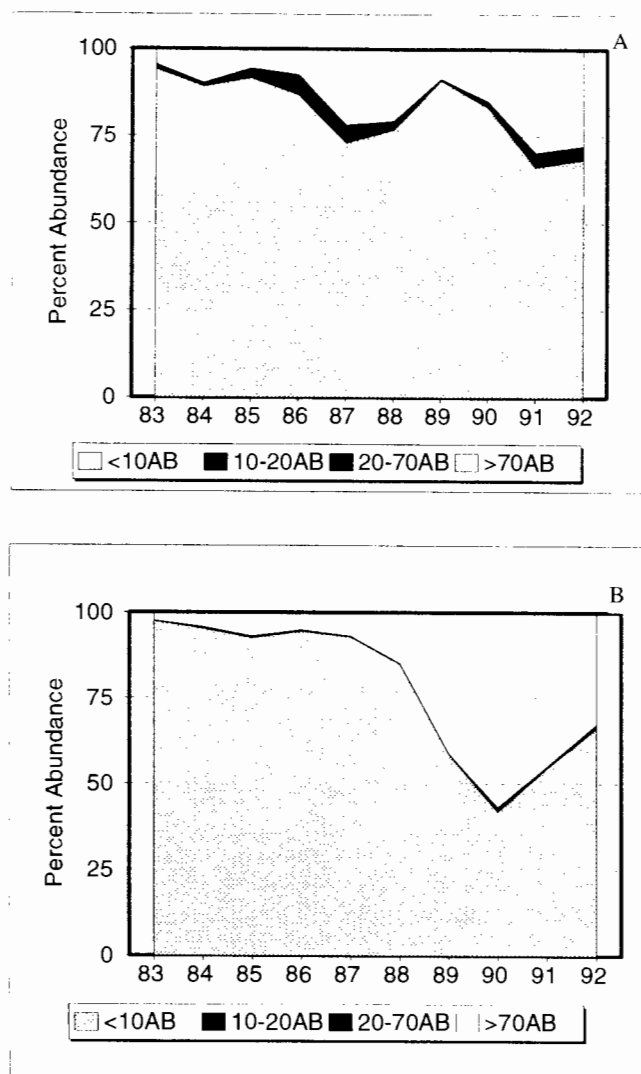


FIG. 5. Relative abundance of spring (A) and summer (B) phytoplankton size classes (< 10  $\mu\text{m}$ , 10–20  $\mu\text{m}$ , 20–70  $\mu\text{m}$ , > 70  $\mu\text{m}$ ), 1983–1992. AB refers to abundance.

increasing in relative abundance in Lake Michigan in the 1960s. In the nearshore area, a shift from oligotrophic forms to those which dominate under eutrophic conditions was evident. Occurrence of certain eutrophic species was also evident in offshore waters. During the 1983 to 1992 period studied here, a shift in diatom species in offshore waters was identified, but it was a shift in dominance from one mesotrophic indicator species to another, not a shift between trophic types. Using the mean spring and summer phytoplankton biomass as an indicator

of trophic status, Lake Michigan offshore waters (1983–92 mean = 0.54  $\text{g}/\text{m}^3$ ) would be classified as oligotrophic (0.5–1.0  $\text{g}/\text{m}^3$ ; Munawar and Munawar 1982). However, the number and high biomass of mesotrophic indicator diatom species, suggests a mesotrophic status. From 1983 to 92, mesotrophic diatoms accounted for 47.2% of the total phytoplankton biomass. Furthermore, the lack of a trend in the ratio of mesotrophic to eutrophic diatom species (Table 10) suggested that the water quality of Lake Michigan has not changed during the 1983 to 92 period. Tarapchak and Stoermer (1976) classified the waters of Lake Michigan during the late 1960s and early 1970s as mesotrophic based on chlorophyll *a*, total phosphorus, primary productivity, and transparency. Similarly, Bartone and Schelske (1982) believed that the open waters of Lake Michigan in 1976 to be either in the upper range of oligotrophic or mesotrophic based on particulate phosphorus concentration.

#### Historical Comparisons—Changes in Algal Species Composition and Size Composition

In the spring of 1963, diatoms were overwhelmingly the most numerous phytoplankton group in southern Lake Michigan (Stoermer and Kopczynska 1967). Similarly, in the spring of 1983 and 84 (Fahnenstiel and Scavia 1987b) and in every year of our study (1983 to 1992) with the exception of 1989, diatoms were overwhelmingly dominant in the spring. The diatoms constituted from 26% (1989) to 94% (1986) of the total spring algae biomass.

During thermal stratification, diatoms were the dominant phytoplankton group in the mid 1960s (Schelske and Stoermer 1972). By the summers of the late 1960s and through the 1970s, blue-green and green algae became dominant (Rockwell *et al.* 1980, Bartone and Schelske 1982). Increased ambient phosphorus concentrations had allowed silica levels to be depleted by the summer, resulting in dominance by non-diatom species (Schelske and Stoermer 1972). For example, in late July and August of 1976 to 78, blue-green and green algae accounted for over 50% of the total biomass (Bartone and Schelske 1982). In 1982, blue-green algae were still predominant in the summer accounting for 32% of the biomass, but by 1983 and 84 they accounted for less than 4% of the biomass at an offshore site near Grand Haven. Instead, phytoflagellates were prominent in the summer accounting for 91% and 68% of the summer biomass (Fahnenstiel and Scavia 1987b). The lake-wide data of this

**TABLE 8a.** Mean spring water chemistry for Lake Michigan 1983–1992. N/P ratios are by weight.

Year	Temperature (°C)	N:P	Silica (mg SiO <sub>2</sub> /L)	Nitrate (mg N/L)	Total Phosphorus (µg P/L)
1983	3.69	76	1.06	0.25	5.3
1984	2.17	84	1.19	0.25	5.3
1985	2.48	71	1.17	0.29	5.5
1986	2.82	110	1.03	0.29	5.6
1987	3.24	88	0.98	0.28	4.8
1988	2.37	84	1.18	0.28	4.8
1989	1.70	86	1.19	0.30	5.2
1990	2.40	92	1.30	0.29	5.1
1991	3.06	91	1.45	0.30	4.5
1992	2.91	114	1.28	0.29	3.5

**TABLE 8b.** Mean summer water chemistry for Lake Michigan 1983–1992. N/P ratios are by weight.

Year	Temperature (°C)	N:P	Silica (mg SiO <sub>2</sub> /L)	Nitrate (mg N/L)	Total Phosphorus (µg P/L)
1983	20.89	119	0.12	0.17	2.9
1984	20.92	92	0.20	0.16	3.7
1985	19.89	112	0.09	0.16	3.2
1986	20.77	79	0.07	0.16	3.9
1987	20.56	107	0.09	0.15	3.6
1988	22.22	106	0.07	0.14	2.8
1989	19.73	74	0.06	0.17	4.2
1990	18.75	65	0.10	0.17	4.6
1991	20.68	99	0.06	0.16	2.4
1992	19.03	93	0.10	0.15	3.5

study support the concept of a shift in summer species composition to flagellates. For the 10-year period, flagellates predominated (Fig. 8) and represented 52.2% of the summer phytoplankton biomass, which is slightly lower than the range observed in 1982 to 84 (55–91%) by Fahnenstiel and Scavia (1987b). However, after 1987 the relative abundance of the > 70 µm size class increased (Fig. 5B) as the abundance of the colonial blue-green algae *Aphanothece* spp. and *Anacystis* spp. increased, while the flagellates *Chromulina* sp. and *Ochromonas* sp. decreased in abundance (Fig. 4).

#### What are the Relative Impacts of Top-down and Bottom-up Effects on Algal Size Composition?

Bartone and Schelske (1982) argued that the changes observed in size composition were most likely associated with nutrients and physical factors

(day length, mixing depth, temperature). Tilman *et al.* (1982) demonstrated that nutrient supply ratios were important factors controlling the relative abundance of phytoplankton. Brooks *et al.* (1984) suggested the variability in Lake Michigan alewife abundance through size selective predation affected zooplanktivory which affected the size structure of the phytoplankton community. Fahnenstiel and Scavia (1987a and b) suggested that at least two factors, nutrient supply and food web interactions, contributed to the shift in the summer epilimnetic phytoplankton community of Lake Michigan. By employing canonical correspondence analysis (CCA) and a joint plot, quantification and visualization of the influence of multiple limnological variables on the relative abundance of phytoplankton size classes over the 10-year study period was conducted. It must be recognized that these data are potentially limited by the infrequent seasonal sam-

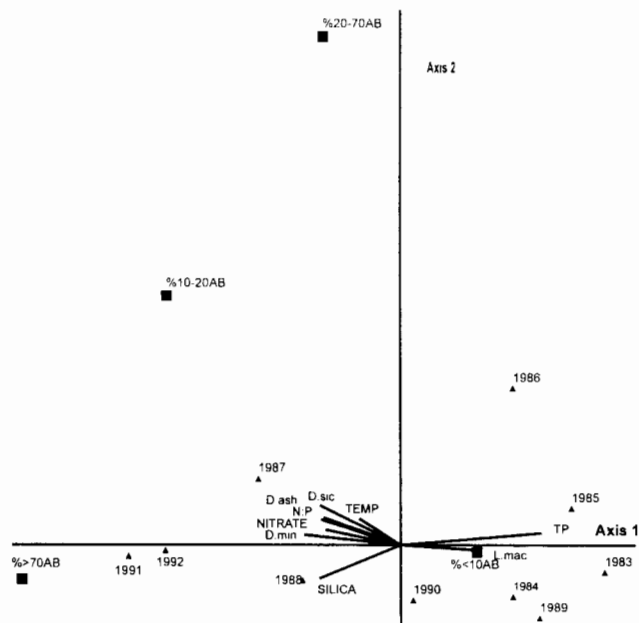


FIG. 6. Spring CCA ordination joint plot showing limnological variables (lines), phytoplankton abundance (AB) by size classes and years of sampling (1983–1992). *D. min* = *Diaptomus minutus*, *D. ash* = *D. ashlandi*, *D. sic* = *D. sicilis*, *L. mac* = *Limnocalanus macrurus*.

pling. Algal reproductive rates are about one division per day while the zooplankton doubling period ranges from a few weeks in the cladocerans to several months in the copepods. These organisms respond at differing rates to changes in the environmental variables.

### Spring

In the joint plot (Fig. 6), the length of the total phosphorus arrow clearly indicated that total phosphorus (TP) was the most important limnological

TABLE 9. Pearson (*r*) correlation of summer and spring phytoplankton size class percent abundance with ordination axis 1.

	Spring <i>r</i>	Summer <i>r</i>
0–10 $\mu$ m	0.99	1.00
10–20 $\mu$ m	–0.74	–0.64
20–70 $\mu$ m	–0.16	0.17
>70 $\mu$ m	–0.99	–1.00

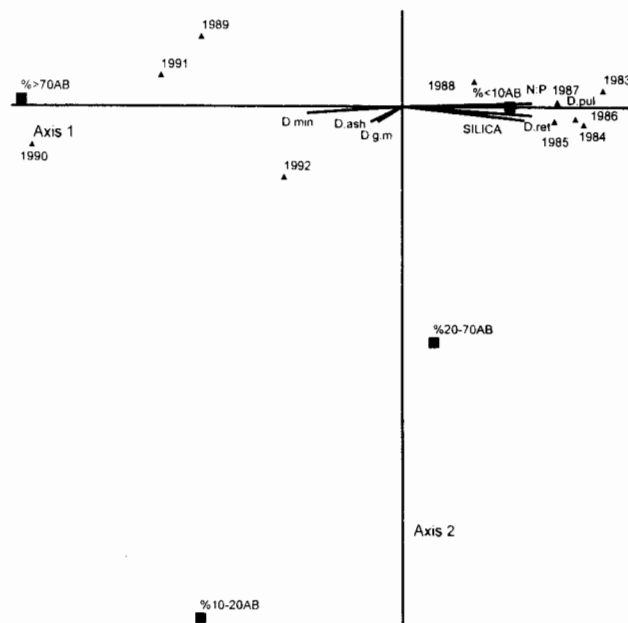


FIG. 7. Summer CCA ordination joint plot showing limnological variables (lines), phytoplankton abundance (AB) by size classes and years of sampling (1983–1992). *D. min* = *Diaptomus minutus*, *D. ash* = *D. ashlandi*, *D. ret* = *Daphnia retrocurva*, *D. pul* = *D. pulicaria*, *D.g.m.* = *D. galeata mendotae*.

variable in the spring data set. TP was strongly correlated with environmental axis 1 ( $r = 0.85$ ) (Table 11a). Abundance of *Diaptomus minutus* explained the next largest variation and was also correlated with axis 1 ( $r = -0.58$ ). Lines of other associated zooplankton (*Diaptomus ashlandi*, *D. sicilis*) followed similar trajectories as *D. minutus*. The positioning of the diaptomid species, silica, and the N:P ratio indicated that they were inversely related to TP. Years were also positioned in relation to the limnological variables. Because axis 1 is highly correlated with the 0–10  $\mu$ m and the > 70  $\mu$ m size classes, which are inversely related, years positioned on the right side of the joint plot have high relative abundance of the 0–10  $\mu$ m size class and low relative abundance of the > 70  $\mu$ m class. Years positioned on the left side of the joint plot have low relative abundance of the 0–10  $\mu$ m size class and high relative abundance of the > 70  $\mu$ m class.

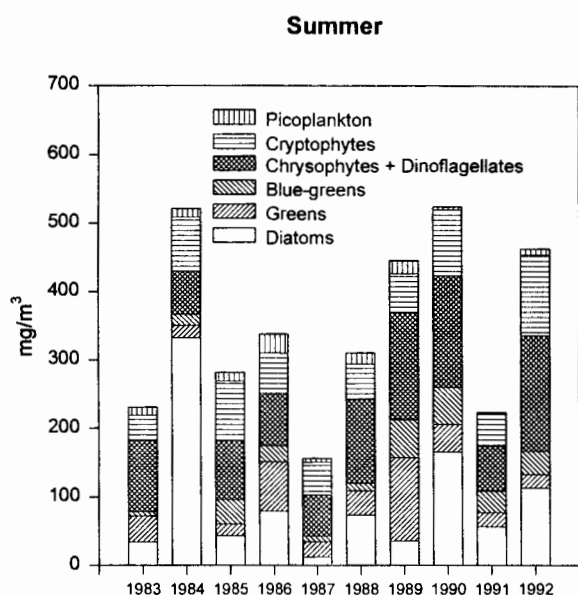
Because TP and *Diaptomus minutus* were the two most important variables in this data set, their influence on relative abundance of phytoplankton size classes was examined. The line representing TP



**TABLE 10.** Distribution of indicator diatom species in Lake Michigan. The classification scheme of Tarapchak and Stoermer (1976) was utilized. M1 = mesotrophic but intolerant of nutrient enrichment, M2 = mesotrophic and tolerant of moderate nutrient enrichment, E = eutrophic. 1970–71 (offshore samples) and 1977 (nearshore samples) data are from Holland (1980) and Stoermer and Tuchman (1979) and represent data from three seasons: spring, summer, and autumn. Values in the columns M1, M2, and E represent April to November values in 1970–71 and 1977. From 1983–92, only spring and summer values are used. All occurrences of organisms are considered.

Date	M1	M2	E	M1+M2/E
1977				
(Nearshore)	8	6	12	1.2
1970–71 <sup>1</sup>	6	3	5	1.8
1983	9	6	8	1.9
1984	9	7	12	1.3
1985	9	6	11	1.4
1986	8	6	8	1.8
1987	8	6	10	1.4
1988	7	6	10	1.3
1989	8	6	10	1.4
1990	8	6	10	1.4
1991	8	6	9	1.6
1992	9	6	10	1.5

<sup>1</sup>Only "major" species are classified.



**FIG. 8.** Summer biomass of divisions of algae in Lake Michigan, 1983–1992.

**TABLE 11a.** Intraset correlations of spring environmental variables on axis 1.

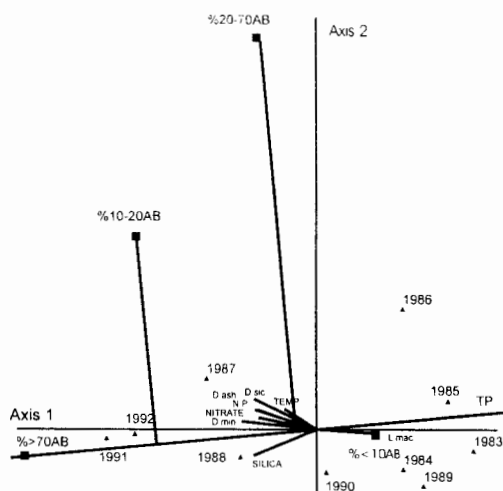
	r
<i>Diaptomus sicilis</i>	-0.49
<i>D. minutus</i>	-0.58
<i>D. ashlandi</i>	-0.47
<i>Limnocalanus macrurus</i>	0.44
Temperature	-0.25
Silica	-0.49
Nitrate	-0.45
Total Phosphorus	0.85
N:P	-0.48

**TABLE 11b.** Intraset correlations of summer environmental variables on axis 1.

	r
<i>Bosmina longirostris</i>	0.27
<i>Daphnia pulicaria</i>	0.60
<i>Daphnia galeata mendotae</i>	-0.16
<i>Daphnia retrocurva</i>	0.64
<i>Diaptomus minutus</i>	-0.48
<i>Diaptomus ashlandi</i>	-0.12
Silica	0.61
Total Phosphorus	-0.29
N:P	0.64

was extended in both directions and a perpendicular was drawn from each size class to the TP line (Fig. 9). That analysis provides evidence that high concentrations of TP were associated with high relative abundance of the size class 0–10  $\mu\text{m}$ , the size class that accounts for over 65% of the phytoplankton abundance. The > 70  $\mu\text{m}$  size class was inversely related with concentration while other size classes were not as strongly associated with TP concentration. Phosphorus is generally considered the limiting factor of phytoplankton growth in freshwater systems.

A similar graph could be constructed for *D. minutus*, which was inversely related with the 0–10  $\mu\text{m}$  size class and positively correlated with the > 70  $\mu\text{m}$  size class. *Diaptomus minutus* and *D. ashlandi* are size-selective feeders and prefer nanoplankton less than 20  $\mu\text{m}$  in size (Bowers 1977, 1980; McNaught 1978; Richman *et al.* 1980). The inverse relationship between *D. minutus* and the 0–10  $\mu\text{m}$  size class can be interpreted as evidence of feeding of this organism on the 0–10  $\mu\text{m}$  size class. Other zooplankton (*D. ashlandi* and *D.*



**FIG. 9.** Positioning of phytoplankton size classes as abundance (e.g. % < 10 AB) along the total phosphorus line of the spring ordination. The position of the size class along the line indicates the approximate ranking of the weighted averages of size class abundance with respect to total phosphorus.

*sicilis*) were inversely correlated with the 0–10  $\mu\text{m}$  size class (Fig. 6), and could be examined as above, although the relationship would be weaker.

#### Summer

Over the 10-year study period, populations of large species of *Daphnia* spp. and *Diaptomus* spp. increased and decreased in response to planktivory by alewife, bloater chub, and perhaps *Bythotrephes cederstroemi* (Makarewicz et al. 1995). No limnological variable expressed itself as the single most important variable affecting phytoplankton size class abundance. Instead several limnological variables had relatively similar lengths in the joint plot (Fig. 7) and thus similar impact on size classes with correlations values ranging between 0.4 and 0.6 on axis 1. These limnological variables included *Daphnia pulicaria* ( $r = 0.60$ ), *Diaptomus minutus* ( $r = -0.48$ ), *Daphnia retrocurva* (0.64), silica concentration (0.61), and the N:P ratio (0.64) (Table 11b). Lower inverse correlations were observed with *Daphnia galeata mendotae* ( $-0.16$ ) and *Diaptomus ashlandi* ( $-0.12$ ). The positioning of *Diaptomus minutus*, *D. ashlandi*, and *Daphnia galeata mendotae* indicated that their abundance was inversely related to the N:P ratio.

In interpreting the relation between phytoplankton abundance, nutrients, and zooplankton abundance, the 0–10  $\mu\text{m}$  and > 70  $\mu\text{m}$  size classes were considered because the percent abundance of the 10–20  $\mu\text{m}$  and 20–70  $\mu\text{m}$  size classes varied by less than one percentage point over the entire 10-year period. The joint plot provides evidence that the relative abundance of the 0–10  $\mu\text{m}$  size class was inversely related to abundance of *Diaptomus minutus* and more weakly inversely associated with abundance of *D. ashlandi* and *Daphnia galeata mendotae*. As before, the inverse relationship was interpreted as evidence of a grazing effect. The joint plot also indicated an association among nutrients, N:P ratios, and silica concentration and the 0–10  $\mu\text{m}$  and > 70  $\mu\text{m}$  size classes.

These limnological gradients also reflect temporal changes in phytoplankton size class relative abundance. Two clusters of yearly samples were evident from the summer joint plot (Fig. 7). In the first cluster, from 1983 to 1987, abundance of the 0–10  $\mu\text{m}$  size class was high while abundance of the > 70  $\mu\text{m}$  size class was low (Fig. 5b). 1988, which is positioned between both clusters, represents a transition year in zooplankton community structure. *Daphnia pulicaria* and *D. retrocurva* were observed only in the first cluster of sample years (1983–1987) and were positively correlated with axis 1 and the 0–10  $\mu\text{m}$  and 10–20  $\mu\text{m}$  size classes (Table 11b). This was surprising as abundance of the 0–10  $\mu\text{m}$  size class would be expected to decrease with higher abundance of large *Daphnia* (Elser and Goldman 1991). However, the relative abundance of the 0–10  $\mu\text{m}$  size class of phytoplankton remained the same from 1983 to 1987 when *D. pulicaria* and *D. retrocurva* were present and often abundant. Lehman (1988) had earlier concluded that the change in *D. pulicaria* abundance did not affect biomass, as indicated by chlorophyll levels, from 1985 to 1987. *Diaptomus minutus*, *D. ashlandi*, and *Daphnia galeata mendotae* abundance was lower in this first cluster and negatively correlated with the 0–10  $\mu\text{m}$  size class.

In response to planktivory by alewife, bloater chub, and the newly arrived exotic *Bythotrephes cederstroemi*, the entire crustacean zooplankton community changed from a complex of *Daphnia* species (*D. pulicaria*, *D. retrocurva*, and *D. galeata mendotae*) and diaptomids (*Diaptomus minutus* and *D. ashlandi*) to a zooplankton community, represented by the second cluster of yearly samples (1989–92), dominated by only *Diaptomus minutus* and *Daphnia galeata mendotae*. After

1988, when populations of *Daphnia galeata mendotae*, *Diaptomus minutus*, and *D. ashlandi* increased, negative correlations with the 0–10  $\mu\text{m}$  size class and positive correlations with the > 70  $\mu\text{m}$  size class were observed. It is during this period that abundance of the herbivorous diaptomids and the filter feeder *D. galeata mendotae* (feeding size range: 1–40  $\mu\text{m}$  size range of algae, Burns 1969) increased to a 10 year high (Makarewicz *et al.* 1995), that abundance and relative abundance of the 0–10  $\mu\text{m}$  size class decreased, and that the > 70  $\mu\text{m}$  class increased in importance in the lake (Fig. 5b). Others have demonstrated the influence of the herbivorous *Daphnia* on small edible phytoplankton (e.g., Elser and Goldman 1991). Similarly, Fahnenstiel and Scavia (1987b) attributed the changes in species composition in 1982 and 1983 as evidence of changes in higher trophic levels: that changes in the *Daphnia* community (Evans and Jude 1986) were a likely cause of the summer phytoplankton compositional changes. As previously mentioned, *Diaptomus ashlandi* and *D. minutus* are size selective feeders and prefer nanoplankton less than 20  $\mu\text{m}$  in size.

The > 70  $\mu\text{m}$  size class, which includes filamentous and colonial algae and large unicells, increased in abundance from less than 2,500 cells/mL (7% of the community) in 1983–1987 to over 7,000 cells/mL (55% of the community) after 1989 (Fig. 5b). Although there is some experimental evidence that diaptomids and *Daphnia* could manipulate and breakdown colonial and filamentous algae (Vanderploeg *et al.* 1988, Williamson and Vanderploeg 1988), these large colonial and filamentous algae (> 70  $\mu\text{m}$  size class) are not readily grazed by herbivorous zooplankton.

The > 70  $\mu\text{m}$  size class, which contains the filamentous and colonial Cyanobacteria, decreased as the N:P ratio increased. A lower N:P ratio is known to favor Cyanobacteria (e.g., Smith 1983). Silica and the 0–10  $\mu\text{m}$  size class was strongly positively correlated with axis 1 (Tables 9 and 11b) which was somewhat surprising since diatoms represented only a small portion of this size class. Silica requirements for diatom growth in Lake Michigan are well known (e.g., Schelske and Stoermer 1972).

Scavia *et al.* (1988) concluded that the summer plankton community of Lake Michigan was controlled largely by predation. Modeling of the food web predicted a return to a plankton community similar to that of the 1970s with *Diaptomus* dominated zooplankton and a substantial filamentous blue-green component under a scenario of increas-

ing invertebrate predation by *Bythotrephes cederstroemi* (Scavia *et al.* 1988), a new zooplankton species for Lake Michigan. In fact after 1989, an increase in the relative importance of the > 70  $\mu\text{m}$  size class (filamentous and colonial algae and large unicells) was observed that was associated with an increase in the abundance of *Diaptomus minutus* and *Daphnia galeata mendotae* and a decline in the N:P ratio in Lake Michigan. In particular, the blue-green algae *Anacystis* and *Aphanothece* became substantially more prevalent from 1983 to 1992.

In summary, the relationship between limiting nutrients and phytoplankton abundance and the relationship between zooplankton grazers and phytoplankton abundance and composition have generally been investigated independently of each other. In this study, canonical correspondence analysis evaluated the influence of multiple limnological variables, including nutrients and grazing, simultaneously on phytoplankton size class structure. Key zooplankton species and nutrients affecting phytoplankton size class abundance were identified and their impacts, which varied over the 10-year study period, were quantified. Primary determinants of relative abundance of phytoplankton size class included nutrients (silica, total phosphorus, and N:P ratio) and abundance of some species of zooplankton. Specifically, *Diaptomus minutus*, *D. ashlandi*, *D. sicilis*, and *Daphnia galeata mendotae* were inversely correlated with the 0–10  $\mu\text{m}$  size class, which was interpreted as a grazing effect on phytoplankton size structure, and positively correlated with an increase in the > 70  $\mu\text{m}$  size class of phytoplankton. Since large zooplankton, such as *Diaptomus* and *Daphnia*, are removed by selective feeding planktivores and *Bythotrephes* in Lake Michigan, changes in the planktivore fish community appear to have affected phytoplankton composition.

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